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PATTERNS OF SPECIES DIVERSITY ON CORAL REEFS¹

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INTRODUCTION

The zonation of dominant species and growth forms on coral reefs is one of the most striking patterns found in any natural community (42, 46, 115). Numerous factors may be important in controlling coral distributions and species diversity. These include light, usually correlated with depth; sedimentation; temperature; wave energy; plankton availability; frequency of mortality caused by storms or tidal exposure; and grazing by fish and urchins. Three major studies that correlate variation in physical factors with coral diversity and species composition over depth and horizontal position conclude that the reef environment is extremely heterogeneous and that species composition and diversity are determined not by physical gradients but by microhabitat conditions and complex biotic interactions (19, 88, 89).

In spite of the heterogeneity of coral reefs strong evidence suggests that predictable patterns of species diversity exist along a depth gradient. Three separate studies on well-developed reefs have found similar patterns of species diversity in relation to depth. On each reef, diversity (measured by species richness and/or H') was low near the surface and increased to a maximum between 15 and 30 m in depth. (Red Sea 0-30 m (74); Jamaica 0-30 m (58); Jamaica 15-56 m (72); Indian Ocean 0-60 m (108). Below 30 m, diversity decreased gradually at the two sites where deeper surveys were made.

Coral reefs have been described recently as being nonequilibrium systems, where competitive exclusion is prevented by frequent disturbances, as pre-

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dicted by the *intermediate disturbance hypothesis* (18). In addition, the strong light gradient in these light-dependent communities allows a potential interaction between growth rate and disturbance such as that postulated by Huston (56).

This review evaluates alternative explanations of the apparently general pattern of diversity in relation to depth on coral reefs. The significant effects of disturbances of many kinds on coral reefs are well enough established (18) to conclude that models based on competitive equilibrium are unlikely to apply to coral reef community structures. Therefore, the review concentrates primarily on nonequilibrium mechanisms, although many of the potential equilibrium mechanisms are discussed. The central question of the review is whether the intermediate disturbance hypothesis alone is sufficient to explain the general patterns or whether the interaction of disturbance with growth rate must be considered.

To evaluate these questions, I review published data on the major types of biotic and abiotic disturbances on reefs, as well as factors related to the intensity of competition and the rate of competition-induced population changes. Where possible, I describe experiments that address these questions. However, the reef environment is so complex that it is virtually impossible to carry out a field experiment that manipulates only one factor while holding all others constant. At present, the critical experiments have not been carried out that would evaluate all of the questions addressed in this review, and thus consistency of observations with patterns predicted by the hypothetical controlling factors is the strongest test available.

DIVERSITY ALONG A DEPTH GRADIENT

Before the whole-reef studies made possible by the development of SCUBA, biologists believed that coral species diversity decreased monotonically with depth, following the gradient of decreasing light availability (see 132). However, the first systematic study of a well-developed reef found the opposite pattern (74, 76). The reefs near Eilat in the Red Sea extend from a reef flat at the surface to a depth of 40–50 m. In linear transect samples over a depth range of 0–30 m, the number of species per 10-m transect increased from 13 on the reef flat to a maximum of 30 at the deepest site (72). Several diversity indices (H' , J , Simpson's D) show the same pattern of an increase from the surface to a depth of 8–12 m and then relatively constant levels to 30 m (Figure 1a).

At Discovery Bay, Jamaica, the reef extends from the surface to a depth of 60–70 m, where a vertical escarpment occurs (71). Huston (58) sampled from 0–30 m, with the 10-m linear transect technique used by Loya. The study was made in March 1977, before the destruction of much of the upper reef by Hurricane Allen in 1980 (134). Coral species richness was much lower than at Eilat, but the pattern of increasing diversity with depth was nearly identical.

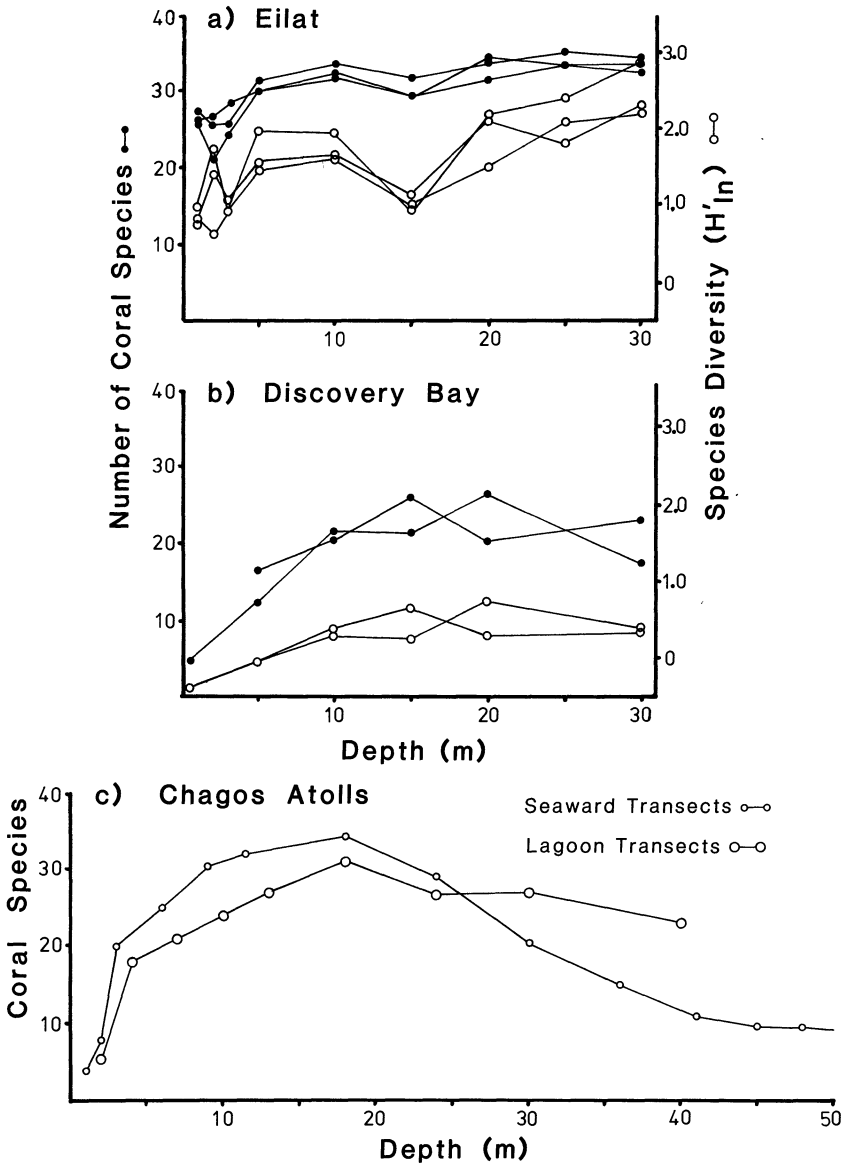


Figure 1 Diversity patterns with depth on three coral reefs. Solid circles represent number of coral species and open circles the H' diversity index (based on natural logarithms). (a) Eilat, Red Sea. Data are means based on three 10-m linear transects from each depth along three depth gradients (74); (b) Discovery Bay, Jamaica. Data were collected as in Loya's study and are from two separate depth gradients (58); (c) Chagos Atolls, Indian Ocean. Data are means based on 10-m transects from 19 seaward depth gradients and approximately 19 lagoon depth gradients (108).

Species richness ranged from 2 species encountered in 30 m of line transect on the reef crest (dominated by *Acropora palmata*) to 17 species per 30 m at a depth of 20 m. General trends were the same in transects on the east and west ends of the fore reef (Figure 1b), and in all groups of organisms.

The pattern of increasing diversity with depth does not continue indefinitely. Liddell et al (72) found that the number of coral species encountered in line transects along the west fore reef slope decreased from 12 at 30 m to 7 at 56 m. Loya (74) reports the number of coral species decreased below 40 m at Discovery Bay. Diversity of photosynthetic organisms apparently begins to decline near 30 m and continues decreasing to the lower limit of photosynthesis.

One explanation for this pattern is that it simply reflects the number of species capable of surviving at any given depth. However, data on the maximum depth range over which each species was recorded (48) indicate that the number of coral species capable of growing at any particular depth actually decreases with depth beginning at 5 m (Figure 2). Even at shallow depths, where diversity is very low, 37 species have been found. The number of species encountered in the transects appears not to be limited by the size of the species pool at shallow depths. However, the decrease in diversity below 30 or 40 m does parallel a decrease in the species pool. Apparently physiological limitation (probably due to low light levels) reduces diversity in the deep reef, but it cannot explain the reduced diversity near the surface.

In the Indian Ocean, Sheppard (108) sampled diversity from the surface to a depth of 60 m on two atolls in the Chagos Archipelago. Species richness increased from the surface to around 20 m where it reached a maximum and then declined gradually to the deepest sites. Interestingly, the same pattern existed on the inner slopes of the lagoon (0–40 m) as on the outer seaward slopes (Figure 1c), where disturbance intensities are much greater. As at Eilat and Discovery Bay, striking zones of species dominance existed in the Chagos Archipelago along the depth gradient, but species richness increased and decreased independently of the zones. Details of the patterns at these three sites

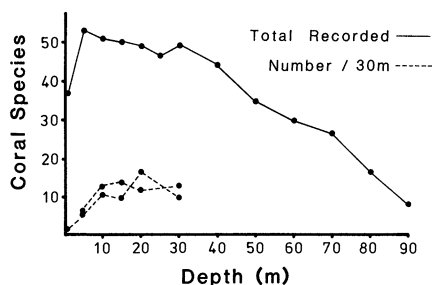


Figure 2 Species pool sizes along a depth gradient for 62 coral species from the north coast of Jamaica (48). Pool size at each depth is the number of species whose recorded depth range includes that depth. The dotted line is the total number of species encountered in 30 m of line transect along two depth gradients at Discovery Bay (58).

will be discussed later in relation to specific factors affecting reef community structure.

Numerous other studies have been made on reefs that span a smaller depth range. Some report an increase in diversity with depth (37, 68, 116), some report a pattern of increase and decrease over a compressed depth range (25), and others report no strong pattern (93).

Two studies that record only a decrease in diversity with depth were both made on submerged reefs where the top of the reef was well below the surface of the ocean and thus did not include the depth range where most increase in diversity occurs on other reefs. Goldberg (41) reported a decrease in coral diversity with depth for a coral reef off southeastern Florida, near the northern limit of reef distribution. The top of the main reef at the study site was 16 m below the surface, and diversity decreased from this depth to 30 m. The highest diversity was observed on isolated patch reefs at 9 m. Ott (89) studied a barrier reef near Barbados that began at 9 m below the surface and extended to a depth of 48 m. The number of coral species encountered along linear transects increased slightly between 9–24 m and then decreased steadily to the maximum depth. Diversity patterns on the outer and inner slopes were nearly identical.

The published data suggest that if suitable substrate is available on a reef slope over the 0–40-m-depth range, coral species diversity sharply increases from the surface to 10–15 m, is highest at 15–30 m, and begins to decline between 25–40 m.

This pattern of low diversity near the surface and highest diversity at intermediate depths cannot be explained by any simple physical gradient. Oxygen, temperature, and salinity do not vary sufficiently with depth to be ecologically significant on a single reef (19, 88, 89) but may be important on a larger scale (38, 40).

The diversity patterns discussed so far have all been related to a depth gradient. However, diversity near the surface is highly variable and shows patterns related to disturbance consistent with the predictions of the intermediate disturbance hypothesis. Although the reef crest is often dominated by one or two species of corals, high diversity can exist on reef crests and shallow reef flats that are periodically exposed at low tides (22, 31, 37) or subjected to other disturbances that cause mortality. High diversity has also been found under conditions apparently unfavorable for coral growth. Ohlhorst (88) recorded the highest diversity at Discovery Bay ($H' = 2.34$) in a very turbid 18-m site within the bay; diversity was also high at 6-m depth in the back reef, where high temperatures and reduced water circulation may negatively affect coral growth.

DISTURBANCES AND NONEQUILIBRIUM COMMUNITY STRUCTURE

Connell (18) emphasized the importance of periodic mortality (disturbance) in preventing competitive dominance and thus maintaining high species diversity,

while Huston (56) made general predictions about diversity levels, based on the interaction of disturbance frequency and growth rate. The basic assumption of the nonequilibrium paradigm is that competition (for relevant resources such as space, light, plankton, etc) is intense and if competitive interactions are allowed to proceed to their conclusion, they will usually result in the elimination of most species and dominance by one or a few, with an associated reduction in diversity. Factors that prevent or slow down this process of competitive exclusion will result in higher diversity. Rapid growth rates will speed up the process if competition is related to growth, so highest diversity is expected at low growth rates that are still adequate to allow survival. Likewise, in the absence of disturbance the competitive process will go to its low-diversity conclusion, so highest diversity is expected when periodic mortality prevents domination by a few species.

Undoubtedly, competition for space is intense on the reef. In shallow water fleshy algae grow rapidly, and cage exclusion experiments indicate that unless grazed by fish and urchins, algae would overgrow and kill the coral (7, 8, 10, 103, 106). In a very basic sense, the existence and growth of coral reefs depend on the reduction of competing algae by herbivores. Kinzie (65) observes, "the strong light in shallow water excludes the deep water species [of gorgonians] by favoring the growth of algae which smother the gorgonians." Corals also grow rapidly near the surface (59), and competitive interactions among corals, based on several mechanisms, have been described and are discussed later.

Abiotic Disturbances

Disturbances can prevent competitive exclusion and thus maintain high diversity among competing species in a wide range of natural systems (18, 21, 32, 50, 73, 81). On coral reefs many types of disturbances can affect diversity. Mortality-causing disturbances are most frequent and intense near the reef surface and decrease in intensity and frequency with depth. Variation in disturbance frequencies near the surface results in a high variability of species diversity at the reef crest.

TIDAL EXPOSURE The consequences of coral mortality that result from occasional extreme low tides are well documented. Fishelson (31) reports that sporadic, extremely low tides in the Red Sea near Eilat kill all or part of the coral population growing on the reef flat. The rapidly growing ($10\text{--}15\text{ cm yr}^{-1}$), branching species (*Acropora*, *Stylophora*, *Pocillopora*) are most sensitive to exposure, but their fast growth compensates for the higher survival of the slowly growing (a few mm yr^{-1}) massive forms. The occasional mass mortality at Eilat apparently maintains the high reef flat diversity by preventing the rapidly growing species from attaining a space monopoly (76). In the absence of disturbances, these same species form monospecific stands over the subtidal

reef flats of the Gulf of Suez, where extremely low tides do not occur. Intermediate levels of diversity exist on reef flats at the southern end of the Gulf of Eilat, which experiences extreme tides less frequently than does Eilat at the northern end.

Glynn (37) found a similar effect on reef flats on the Pacific side of Panama, where extreme tidal exposure killed 40–60% of the dominant species of *Pocillopora* and had a diversifying effect on the reef flat. Nevertheless, diversity on the reef flat was still low in comparison with that on the lower reef slope. Connell (18) noted similar occurrences on Australian reefs, as did Ditlev (22) in the East Indian Ocean. The low tidal amplitude in the Caribbean (42) makes tidal exposure an unimportant factor at Discovery Bay, although the upper parts of colonies are occasionally killed.

WAVE ACTION Wave energy decreases rapidly with depth. Most wave energy is released when the wave breaks and so is concentrated near the reef crest. Water movement is reduced to 4% of the surface movement (diameter of particle orbit at the surface equals wave height) at a depth of one half the wave length. Roberts et al (100) report a 200-fold decrease in wave force from the surface to a 30-m depth ($>10,000 \text{ dynes cm}^{-2}$ to $<50 \text{ dynes cm}^{-2}$) on a reef near Grand Cayman Island, although the increase of current strength with depth compensated for reduced wave energy at this site. The decreasing depth gradient of wave energy is reflected in the effect of Hurricane Allen on the reef at Discovery Bay. Although storm effects were visible to a depth of 30 m, the damage was concentrated on two species (*Acropora cervicornis* and *A. palmata*) in the shallower reef zones (0–15 m; S. L. Ohlhorst & W. D. Liddell, personal communication).

Wave damage can influence reef diversity, through both chronic wave action and the extreme effects of destructive storms. Connell (18) emphasizes the diversifying effect of occasional severe hurricane damage on Australian reefs. Grigg & Maragos (49) found that the degree of exposure to waves and swells affected coral cover and diversity at their 8-m study sites in Hawaii. In general, diversity was highest and cover lowest at the most exposed stations, which indicates that disturbance from chronic wave action can also act to maintain diversity. Although heavy wave action may cause considerable destruction (for example, see 121, 134), some water movement is necessary for coral growth (54, 62, 115, 132).

At Discovery Bay, the frequency of mortality-causing disturbances is apparently too low to maintain high species diversity at the crest. The devastating Hurricane Allen of 1980 was the first major storm in 63 years (86). Thus the patterns of diversity recorded by Huston in 1977 (Figure 1b) had developed during a 60-year period of freedom from major storm disturbance.

Although some disturbance is apparently necessary to maintain high coral

species diversity, diversity may be reduced by extremely frequent or severe disturbances that prevent coral species from surviving. Reef crests subjected to extreme wave action tend to be devoid of corals and are characterized by algal ridges, smooth massive structures covered by encrusting calcareous red algae. Such ridges are well developed in the Indo-Pacific on windward crests (132) and also in the Caribbean (35). Under conditions of less severe wave action, a community of increasing diversity and structural complexity can develop. Wells (132) reports a "richer growth of reef corals" on the crests of leeward reefs where algal ridges are poorly developed or absent. For the Caribbean, Geister (33) defines six "breaker zones" of decreasing wave strength, with diversity highest in the intermediate levels of wave action: (a) the algal ridge; (b) interlocking growth of the hydrocoral *Millepora*, with the matlike colonial zooanthid *Palythoa* and some coral; (c) thickets of massive branching *Acropora palmata*, with *Diploria strigosa* and a few other species; (d) nearly monospecific stands of *A. cervicornis*; (e) nearly monospecific stands of *Porites porites*; and (f) a mixture of backreef and deepwater species. The first five breaker zones encompass a progression from low diversity caused by extreme abiotic conditions (Zones a and b), through relatively high diversity where abiotic conditions (wave disturbance) prevent the expression of competitive dominance (Zone c), to low diversity where competitive dominance is expressed rapidly under conditions of rapid growth and low levels of disturbance (Zones d and e). Zone f, which has very little wave action, does not fit this hypothetical sequence, possibly because the extremely low water circulation or high temperatures often found in back reef areas create conditions unfavorable for coral growth, reducing growth rates and consequently increasing diversity. Grigg (48) reports a similar pattern related to wave exposure on 14 islands across the Hawaiian Archipelago. Diversity was lowest at the extremes of the disturbance spectrum and highest at intermediate levels, as predicted by the intermediate disturbance hypothesis. However, unexpectedly low diversity values were found on some islands where seasonally low water temperatures apparently slowed coral growth.

SEDIMENTATION Both tidal exposure and wave action have their main effect at or near the surface. Sedimentation can be important at any depth. Calcium carbonate produced by coral and calcareous algae is continuously broken up by physical and biological action and transported off the reef by gravity aided by water movement (46). Sedimentation can affect coral by (a) settling directly on the coral and thus interfering with feeding and/or photosynthesis, and (b) reducing the amount of substrate suitable for coral growth by covering hard substrate with shifting calcium carbonate sand. Reefs may also be affected by sediment discharged from rivers. Either alluvial or reef-generated sediment may produce turbidity, which has a major influence on light availability and

will be discussed in a later section. Sedimentation may act both as a disturbance (episodic or chronic) and as a regulator of coral growth rates (23).

Coral species differ in their ability to remove sediment. Hubbard & Pocock (55) analyzed 26 species of coral for their ability to remove sediment particles of different sizes and found strong differences correlated with polyp size and morphology. Large particles are removed by controlled distention, which is most efficient in species with large, complex calices (e.g. *Montastrea cavernosa*). Some corals with small polyps are extremely efficient at removing sediment particles with their tentacles (e.g. *Porites* spp.). Fine sediment is generally removed by ciliary action, and some species that are poor at removing large particles are efficient at removing silt (e.g. *Acropora* and *Agaricia*). As a consequence of these differing abilities, sediment load can have a major effect on the distribution of coral species and, thus, on the composition of the reef community.

In Puerto Rico, Loya (75) reports that coral cover and diversity were reduced in an area which received $150 \text{ g m}^{-2} \text{ day}^{-1}$ of alluvial sediment, in comparison with an area which received only $30 \text{ g m}^{-2} \text{ day}^{-1}$. *Montastrea cavernosa*, a species highly efficient in sediment removal, was most abundant at the site with high sedimentation, whereas *Agaricia*, a poor sediment remover, was much rarer than at sites with lower sedimentation. At Discovery Bay, Jamaica, Ohlhorst (88) reports the same species response at high sediment sites, although no overall correlation existed between sedimentation rate and the size or abundance of particular species. In Barbados, Ott (89) found no significant correlation between sedimentation and either coral biomass or diversity.

Sediment load is highly variable on reefs and depends at least partially on such microsite differences as proximity to resuspendible sediment. Both Ott (89) and Ohlhorst (88) found highest sediment deposition near the surface, where water turbulence is highest, and Ohlhorst reports a significant inverse correlation between sediment deposition and depth. In spite of high resuspension and deposition of sediment near the surface, the largest accumulations of sediment occur deeper in the reef, where hard substrate suitable for coral growth may be covered by sediment. Under these conditions, coral diversity might be reduced by extreme scarcity of suitable substrate or increased by moderate amounts of sediment. In the latter case, unstable sediment between coral colonies could prevent them from growing large enough to interact competitively.

Although coral diversity can be high even where total coral cover is low, the reduction of available substrate by sediment has no predictable effect on coral diversity beyond the simple fact that where little or no suitable substrate is available, few or no species of coral will be found. On a reef flat along the Indian coast, the number of coral species increased from 4 to 22 per 30 m^2 as the coverage of sand and coral debris decreased from 90% to 15% (82). At both

Discovery Bay (58, 72) and Eilat (74), coral species diversity showed no relation to the amount of coral cover (or, inversely, the cover of sand and debris). Highest diversities in particular transects were at coral covers of 30–95%.

Biotic Disturbance

HERBIVORES On coral reefs, the effects of herbivores and corallivores are much more subtle than the dramatic changes caused by tides or storms at the reef crest. The effect of herbivores on a natural reef is so pervasive that it is difficult to detect because few natural controls exist to demonstrate the effect. Only when herbivores are prevented from grazing the reef's surface by natural causes such as turbulence or experimental removal does it become clear that without herbivores the coral would be rapidly overgrown and killed by heavy growth of algae.

The dominant grazers on coral reefs are sea urchins and fish, particularly parrotfish. All urchins and most grazing fish feed primarily on algae. Although in the course of continually scraping algae from the surface of living coral the grazers may damage the coral, only a few species of fish actually feed on coral (87, 98), and these species compose a relatively small portion of the total fish biomass.

Herbivorous fish and urchins have a direct effect on algae and, thus, an indirect effect on coral. The usual effect of grazers is a great reduction in algal biomass, which may still be turning over at a high rate even under intense grazing pressure. Sea urchins, particularly the genus *Diadema*, are conspicuous and important algal grazers on reefs throughout the world. In the Virgin Islands, removal of all the *Diadema antillarum* from an isolated patch reef resulted in a greater than tenfold increase in the algal biomass over a four-month period, compared with results on naturally grazed controls (106). In the Red Sea, *Diadema setosum* can prevent algae from monopolizing space, and a strong inverse correlation exists between *Diadema* density and algal cover (7, 20). Sammarco (103, 105) found the same inverse correlation between algal cover and urchin density in cages with experimentally manipulated *Diadema* densities. Moderate urchin grazing may have a diversifying effect on tropical algal communities similar to that reported (91) for temperate algae and urchins. Higher algal diversity was found in grazed as compared with ungrazed patch reefs in the Virgin Islands (106), where a single algal species dominated the ungrazed system; the opposite result was found at Discovery Bay where no alga was dominant under ungrazed conditions (105).

The interaction of algal palatability and grazing pressure can result in conspicuous shifts in algal species composition (11, 77, 119, 120). A clear example is an increase in encrusting calcareous (coralline) algae under heavy grazing, contrasted with elimination of crustose algae by rapidly growing

filamentous or foliose species under reduced grazing pressure. This shift in species composition has been reported in cases of urchin grazing (7, 106) and in grazing by parrotfish (10). The calcareous algae are a suitable substrate for coral settlement and growth.

Whereas the effect of herbivores on algae is clear, that on corals is more complex. While herbivores make possible the survival of coral that would otherwise be smothered by more rapidly growing algae, herbivores may also kill recently settled coral recruits in the course of thoroughly scraping off algae. Reports suggest that some herbivorous fish avoid eating even very small coral colonies (8, 10), but sea urchins are not so discriminating and destroy coral spats in the course of grazing (103, 104, 107). On a surface with few protected refuges for coral spats, coral survival was highest at intermediate urchin densities; enough algae were removed to prevent corals from being eliminated by competition but scraping damage was not severe enough to damage most corals (103). Where coral recruits are protected from physical damage by spatial refuges such as crevices, coral survival is greater under highest (fish) grazing pressure (10).

Although heavy algal growth can kill coral, moderately high algal densities may reduce the amount of interspecific contact between corals and thus allow survival of coral species that would otherwise be eliminated by competition with other corals. At two 30-m sites at Discovery Bay, Jamaica, coral diversity was highest at the site with high algal cover (46% algal cover, no *Diadema* urchins) and lower at the site with a low cover of fleshy algae (10% cover, *Diadema* present; M. A. Huston, unpublished data). On shallow patch reefs at Discovery Bay, where algal growth is very rapid, coral diversity was highest where urchins were present and algal biomass was low (104).

The importance of urchins as algal grazers may be abnormally great for reefs with heavy fishing pressure, and these are where most of the experimental urchin research has been conducted. Because fishing removes both predators on urchins and herbivorous fish, the relative importance of urchins is much lower for unfished reefs (51). Urchin densities may fluctuate drastically, for reasons not fully understood—shown by the recent massive die-off of *Diadema* in the Caribbean (67).

A special case of algal grazers is the damselfish (Pomacentridae), which creates and defends algal “gardens” growing on dead coral. A damselfish may kill the living coral by nipping away living tissue (63, 126) and may actually “weed” its garden to control the algal species composition (87). Potts (97) found that the algal growth alone is sufficient to kill coral; by overgrowing and shading it, algae cause exhaustion of the coral’s metabolic reserves. The algae that grow on the damaged coral are protected from other herbivores by the aggressive damselfish, although occasionally schools of herbivorous fish may enter the territory and graze heavily, overwhelming the damselfish by their numbers (126).

These fish gardens may cover a substantial portion of the reef surface—up to 60% on reef flats (131)—and significantly affect coral species composition. Massive smooth-surfaced corals grow and recover from fish damage more slowly than the branching species. In the Caribbean, damselfish tend to eliminate the massive *Montastrea annularis* from the upper parts of the reef, which are dominated by the fast-growing branching *Acropora cervicornis* (63). In the eastern Pacific the same phenomenon occurs with the massive species *Pavona gigantea* and the branching species *Pocillopora damicornis* (131). Wellington further observed that *Pocillopora* recruitment and growth are favored in damselfish territories because damselfish protect the area from grazing corallivorous fishes. Damselfish activity is greatest in the upper part of the reef (above 12 m) where algal productivity is highest (126). Damselfish may thus contribute to reduced diversity in the upper reef by increasing the dominance of the branching species at the expense of massive species.

CORALLIVORES A few species of fish feed primarily on coral. These include the pufferfish (Tetraodontidae), triggerfish (Balistidae), butterflyfish (Chaetodontidae), filefish (Monacanthidae), and some of the larger parrotfish (Scaridae) (98). Some of these species browse only the polyps and thus allow the coral to regenerate. Corallivores that break off and ingest portions of the coral skeleton feed primarily on branching species of coral. In the Atlantic the branching species *Acropora* and *Porites* are particularly affected, while in the Pacific such genera as *Pocillopora*, *Acropora*, and *Montipora* are most affected. In the Indo-Pacific, Neudecker (85) found that transplanted *Pocillopora damicornis* colonies were severely grazed at 15 m and at 30 m (no difference between these depths) but were unaffected by grazing at 2.4 m. *Pocillopora damicornis* is rarely found in the deeper parts of the reef, although caged colonies grow faster at 15 m than at 2.4 m. Similar observations were reported by Wellington (131) in Panama, where *P. damicornis* grew better within damselfish territories where it was protected from corallivores. Wellington attributed the dominance of *Pocillopora* in the upper reef to a greater inherent topographic complexity near the surface that provided more suitable habitat for damselfish, whose activities in turn favored *Pocillopora* at the expense of the massive species *Pavona*.

In the upper parts of the reef corallivores may increase diversity by selectively damaging the dominant branching species; deeper, where the same branching species are less abundant, corallivores could decrease diversity. The only data available indicate no difference in corallivorous fish activity between 15 and 30 m, so it is difficult to determine whether there is a gradient in this biotic disturbance or simply a reduction near the surface.

A potentially devastating coral predator is the crown-of-thorns starfish (*Acanthaster planci*). On reefs off the Pacific coast of Panama, *Acanthaster*

selects the less abundant nonbranching coral species and avoids the abundant *Pocillopora*, which harbors symbiotic crustaceans that repulse the starfish (37). Selective destruction of the rarer species results in a significant reduction in species diversity, an effect opposite to density-independent mortality or to selective predation on the most abundant species.

Depth Gradients in Disturbance

Wave energy can affect even the deep reef during severe storms, but the intensity of wave action decreases rapidly with depth. Tidal exposure affects only the shallowest part of the reef, while sediment movement is greatest near the surface but can affect coral at any depth. Thus, the effect of physical disturbance is concentrated at shallow depths and decreases monotonically with depth. Although the relationship between diversity and the depth gradient of abiotic disturbance is consistent with the intermediate disturbance hypothesis, the effect of wave action is so small below 20–30 m, where diversity is highest, that the correlation is probably spurious. This conclusion is reinforced by the observation that diversity increases with depth, even on reefs such as at Discovery Bay where wave action is insufficient to maintain high diversity on the reef crest. Disturbance levels vary greatly among reefs, resulting in a strong gradient of disturbance where wave energy is high or virtually no gradient on protected reefs. Similar levels and patterns of diversity were found on both the inner and outer slopes of a barrier reef (89) and on both the seaward and lagoon slopes of an atoll (108). Thus, diversity increases with depth regardless of the strength of the disturbance gradient.

The effect of biotic disturbance on coral diversity is more complex, because corallivores and herbivorous damselfish can have opposing effects on coral species composition. Since the expected effects of corallivores are opposite those actually found on reefs, they apparently do not exert a controlling influence. While damselfish probably contribute to the dominance of branching coral in shallow waters on some reefs, the same patterns of diversity occur regardless of the presence of damselfish. More work is needed on the interacting effects of corallivores and damselfish and on the possibility that human intervention through fishing has altered the natural pattern. Hay (51) found that herbivory by urchins and fish on turtle grass *Thalassia* increased along the depth gradient on heavily fished reefs but decreased on unfished reefs. On the basis of available information, no depth gradient of either biotic or abiotic disturbance can explain the change in diversity with depth.

COMPETITIVE INTERACTIONS ON THE REEF SURFACE

The various disturbances described in the previous section affect species diversity either by totally eliminating a particular group of organisms or by

reducing the populations of the most abundant species. The rate at which particular species are able to reestablish numerical (or biomass) dominance following a disturbance will determine the effect on species diversity of a particular frequency or magnitude of disturbance. This interaction between disturbance frequency (or magnitude) and the rate at which dominance is achieved can result in a predictable pattern of species diversity (56). As the rate of competitive exclusion increases, a higher frequency of disturbance is required to prevent competitive exclusion and allow species to coexist.

Mechanisms of Competition among Coral

At shallow depths the cover on a reef of coral or other organisms such as encrusting algae often approaches 100%. Under these conditions exploitative competition for resources apparently occurs. Rapidly growing branching coral species achieve dominance by overtopping other corals, reducing light availability and water circulation. This mechanism has been suggested to explain the dominance of pocilloporid corals at shallow depths in the Pacific (39, 94) and of *Acropora* in the Caribbean (111). When free of herbivores, algae can overgrow and "smother" coral as well as other organisms, such as gorgonians (65). Sediment trapped in algal growth or at the base of branching corals may contribute to mortality caused by overtopping.

Another mechanism of interaction among coral that has received considerable attention is extra-coelenteric digestion, which could be classified as interference competition. Lang (66) reported that corals were able to extrude mesenterial filaments capable of digesting the surface of their neighbors, thus winning competitive interactions for space. Lang's experiments showed that a hierarchy of "digestive dominance" exists among Caribbean corals, with position in the hierarchy correlated with polyp size. This hierarchy is inversely correlated with coral growth rate and the ability to overgrow and smother competitors. Thus, these inversely related competitive abilities apparently offered a mechanism to help explain the high diversity on coral reefs in the context of equilibrium competition theory. However, field observations in the Pacific showed a reversal of this hierarchy; *Pocillopora* appeared both fast-growing and digestively dominant (39, 94). Laboratory experiments on the Pacific corals contradicted the field observations and indicated a digestive hierarchy consistent with the results from the Atlantic (36).

These discrepancies were finally resolved by Wellington's (129) long-term experiments; he demonstrated that the previously reported hierarchy based on extension of mesenterial filaments was a short-term response. The short-term results were reversed when the fast-growing species (*Pocillopora*) recovered from the initial damage and produced sweeper tentacles that killed the tissue of the slower-growing species (*Pavona*) and established a buffer zone ultimately covered by encrusting coralline algae. No experimental results have been

reported for an equivalent species pair from the Caribbean (e.g. fast-growing *Acropora* vs digestively dominant *Montastrea annularis*), although *Montastrea cavernosa* can produce sweeper tentacles to defend itself against *Montastrea annularis* (99). Thus, at least for some Pacific corals, the fast-growing species can achieve dominance by both of the major mechanisms—overtopping and digestion. This reduces the probability that diversity can be maintained by a balance of competitive abilities.

Regardless of the specific competitive mechanisms that result in population changes, the interaction of disturbance frequency and the rate of population change can produce a predictable pattern of species diversity. Under conditions where competitive dominance is expressed slowly, environmental changes may cause shifts from one competitive mechanism to another. When this occurs, relative competitive abilities may be reversed but the net effect will still be a slow expression of competitive dominance. Such alteration of competitive hierarchies by changing environmental conditions is an alternative mechanism that could produce the nonhierarchical “circular competitive networks” on the underside of coral shelves reported by Buss & Jackson (16).

Few studies exist of the rates and dynamics of competitive interactions under natural reef conditions. In an 18-month study of interphyletic interactions at 15 m on the reef at Discovery Bay, Jamaica, *Montastrea annularis* lost space in 50% of all encounters with fleshy and encrusting sponges (88). However, *Montastrea* also lost space in 19 of 40 cases in which there was no apparent competitor. Space was maintained in at least half of the encounters with other classes of organisms, including other corals, noncoral coelenterates, algae, and encrusting foraminifera.

Ohlhorst's data (88) provide an important insight into competitive interactions in the deeper reef (15 m). They show a perfect correlation ($r_s = 1.00$, $p < 0.01$, $n = 5$, Spearman's Rank Correlation) between abundance on the reef surface (transect data) and percentage of perimeter contact with *Montastrea* for algae, sponges, noncoral coelenterates, miscellaneous organisms, and bare substrate or sand. The proportionality between interactions (physical contacts) and abundance suggests that coral contacts are essentially random for these organisms, and no positive or negative spatial interactions occur. However, for two classes of organisms, this relationship is significantly nonrandom. For coral the frequency of perimeter contact (at 0–2 cm) is much lower (6.5%) than their abundance on the reef would indicate (48.1%). For the encrusting foraminiferan *Gypsina*, the contacts are much more frequent than would be expected from their abundance (25.6%, compared to 3.2%). These data, together with Wellington's (129) observation that coral border zones killed by sweeper tentacles are colonized by encrusting calcareous algae (ecological equivalents in shallow water of the encrusting foraminifera), indicate that coral may avoid interspecific interactions by establishing border zones maintained by encrusting

organisms. In a sample of 101 coral-*Gypsina* contacts over 1.5 yr, 60% of the contacts showed no change, while coral lost space in 20% and gained space in 19% (88). Thus, once space is occupied, intercoral competitive interactions may be greatly reduced and stable spatial relationships established.

Changes in coral colony size that result from competitive interactions (primarily digestive) occur slowly at 15 m; therefore, a low frequency of disturbance would be adequate to prevent competitive equilibrium and maintain species diversity. Such spatial stability and slow rates of change are less likely to be found at shallower depths, where rapid growth and overtopping provide an alternative mechanism of competitive interactions.

The Light and Growth Gradient

The amount of light reaching the reef decreases with depth and produces a gradient in the productivity and growth of the reef organisms. Even in the clear tropical waters where coral reefs are found, light intensity is reduced 60–80% in the top 10 m of water (65, 89). Inevitably, the total energy available for all life processes of autotrophs is also reduced with depth, although the presence of photosynthetic algae and coral at depths of 60 m or more indicates that even extremely low light levels are sufficient to support some growth.

Because reef-building corals are basically photosynthetic organisms, the energy they have available for all life functions depends primarily on the amount of light they receive, although most coral species are partially heterotrophic and ingestion of zooplankton may partially compensate for low light levels. All species of reef-building corals have algal endosymbionts (zooxanthellae), and their photosynthesis has been shown to enhance calcification (64, 43). Light-to-dark calcification ratios ranging from 3.2–22.9 for 11 species of corals were reported by Goreau & Goreau (45), and similar values have been found in many other studies (6, 44, 92, 122, 135). There is even a report of a negative correlation between coral growth rate and cloud cover (38).

In addition to coral, many reef organisms depend on light for growth. Photosynthetic algal endosymbionts are also found in shallow-water gorgonians (65); colonial anthozoans, such as *Zooanthus*; and species of such diverse phyla as molluscs, flatworms, and sponges. Various types of macroalgae are also important components of the reef community. All of these organisms depend directly on light for energy, although they may also be partially heterotrophic.

The presence of annual density variation in the calcium carbonate skeleton produced by coral (analogous to growth rings in temperate trees) allows the rapid determination of the rate of coral growth (linear extension of the CaCO_3 skeleton) by X-radiography (14, 24, 78). The annual nature of these bands is well established (12, 14, 52, 127), although not all species have detectable bands, and even within a species that has bands, not all colonies show distinct

banding (59, 128). For many species direct physical measurement of growth over a period of time is the best technique, although it is much more time consuming than X-radiographic measurement, particularly for deep-water corals. The measurement of coral growth is reviewed by Buddemeier & Kinzie (13) and Bak (3).

Results from numerous studies (5, 6, 14, 34, 59, 128, 133) support the generalization that coral growth rates decrease with depth within a species, although there are species that show no such trend. Because of photoinhibition by intense light at the surface, the optimal level of light usually occurs slightly (a few centimeters or decimeters) below the surface (15, 117), and from the surface to 2–5 m growth of some species increases slightly (26, 27, 59, 121).

When the growth differences by depth are compared between species rather than within a species, the pattern is much stronger. The fastest-growing coral species predominate in shallow water, and slower-growing species increase in abundance with depth. Decreasing growth rates, resulting from the decrease in light with depth, affect not only reef-building corals but also all of the organisms dependent on photosynthesis, including algae (Figure 3) and gorgonians (65).

Light availability may also influence coral morphology, in a manner analogous to the multilayer/monolayer strategies described by Horn (53) for terrestrial tree communities. The dominant deepwater corals grow as flat horizontal plates or shelves, while the same or related species may grow as vertical plates, columns, or spheres in the upper parts of the reef. Extensive beds of branching (multilayer) species are often found in shallower water. Physical disturbance also has a major effect on growth forms and species distributions, most obviously in excluding less robust forms from areas with high wave energy.

Light is not the only source of nutrition for coral. All species of reef-building corals are at least partially heterotrophic, feeding primarily on zooplankton (47, 61, 84, 95, 96). The degree of heterotrophy seems to be positively correlated with polyp size (96), and species with large polyps are more abundant in the deep reef. The fast-growing corals that dominate the upper parts of most reefs have small polyps and presumably depend much more on photosynthesis than on plankton feeding. Experiments with the effect of light and plankton availability on the growth of three species of coral at two depths (1–2 m and 7–10 m) support Porter's generalization about the relationship of polyp size to heterotrophy (130). For the three species that Wellington examined, reduced light at the deep sites resulted in a greater decrease in growth than did reduced plankton, suggesting that plankton feeding does not compensate for reduced light at deep sites.

Glynn (35) has demonstrated that plankton levels can be significantly reduced as water passes over a reef and also reports that *Pocillopora* growth in the

Gulf of Panama was significantly correlated with the monthly means of zooplankton standing crop over a 56-month period (38). Zooplankton are more abundant over reefs than in nearby open ocean (29, 102), and the abundance and composition of the plankton may vary from one type of reef substrate to another (e.g. coral versus sand; see 1). The available information indicates that plankton availability decreases with depth (88; S. L. Ohlhorst, unpublished information) and might thus complement the effects of the light gradient.

In summary, a strong gradient in light energy and thus in autotrophic productivity occurs on all coral reefs. Slight variation may occur with cloud cover or water clarity, but the overall pattern of the light extinction curve is the same on all reefs. This nearly constant gradient of light contrasts with the disturbance gradient, which is highly variable because it depends on the strength of wave action impinging on the reef.

Consequence of Reduced Growth Rates in the Deep Reef

Reduced competition for space under low-light conditions apparently allows the survival of slow-growing, "shade-tolerant" species that are unable to compete successfully in the high productivity environment of the upper reef. Most of these species are not physiologically limited to a particular depth and can survive in shallow water under certain conditions, such as in turbid areas or in caves.

The dramatic reduction of algal biomass with depth (Figure 3) has consequences for all sessile organisms, which are very small when they settle out of

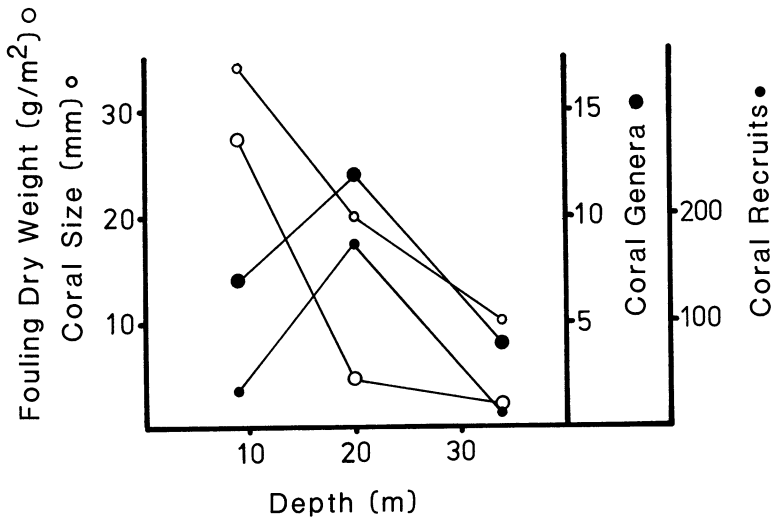


Figure 3 Relationship between algal biomass and coral recruitment, diversity, and size along a depth gradient. Based on data in Birkeland (8).

the plankton and must compete with algae and other organisms for space. Vine (126) found that the number of featherduster worms (*Serpulidae*) settling on unprotected plates remained close to zero from the surface to a depth of 15 m, where algal productivity decreased rapidly. Below 15 m the number of serpulids that settled increased sharply until 25 m where it began to decrease because of the sedimentation.

Birkeland (8) studied coral recruitment on artificial substrates at depths of 9–34 m on both the Caribbean and Pacific coasts of Panama. As in Vine's study, the biomass accumulation of filamentous algae dropped dramatically with depth. Associated with this reduction in algal biomass was a fivefold increase in the number of surviving coral recruits between 9–20 m and an increase in the number of identified coral genera from 7–12 m. Although the coral grew fastest at the 9-m site, their survival was greatest at 20 m, where algal growth was less. At both the 9- and 20-m sites coral survival and growth were greatest on the vertical sides of the settlement blocks, where light availability (and algal biomass) was lower than on the upper surface. At 34 m coral grew only on the upper surface.

Birkeland (8) suggests that diversity differences between reefs show the same relationship to the productivity of algae (and other "fouling community" organisms) as is found along the depth gradient. The lowest rates of biomass accumulation (at a 9-m depth) among five different reef sites were on the high-diversity reefs of the San Blas Islands on the Caribbean coast of Panama. The extremely high productivity of the fouling community (including barnacles, bryozoans, and tunicates) in nutrient upwelling areas on the Pacific coast effectively prevented the survival of any coral recruits (8). The artificial substrates used in Birkeland's experiments were not protected from grazing; thus, the biomass differences may reflect differential herbivore pressure as well as different rates of productivity. This does not, however, affect the conclusion that coral recruitment, growth, and diversity can be greatly reduced by competition from dense growth of algae and other organisms.

Reduced light levels caused by turbidity in shallow parts of a reef are sometimes associated with species composition and morphology more typical of the deep reef (2, 9), although very high turbidity can eliminate coral. Loya (75) reports reduced coral cover and diversity in an area where both turbidity and sedimentation rates were high (20-m depth). Roy & Smith (101) also report a reduction in cover and diversity in an area with high turbidity (8-m depth). However, out of 10 sites studied near Discovery Bay, Jamaica, Ohlhorst (88) found the highest coral diversity ($H' = 2.34$, $J' = 0.81$) at an 18-m site that was "very turbid, with visibility often less than 5 m." At this site, coral cover was the lowest (18%) and the diversity of both fleshy and encrusting sponges was the highest recorded at any of the 10 sites. Over the 10 sites, sedimentation was positively correlated with species diversity, and Ohlhorst

suggests that sediment may have a diversifying effect similar to that of predators. Although this site is within the depth range at which species diversity is generally highest, these results indicate that certain levels of light reduction and other stresses associated with turbidity and sedimentation do not necessarily reduce coral species diversity, but may actually increase it.

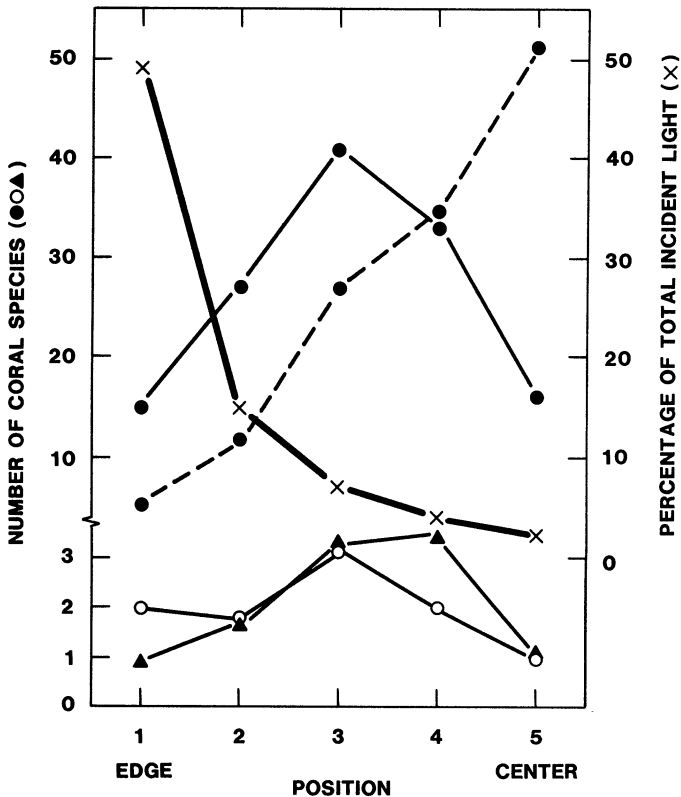
The effect of light on the species composition (and ultimately diversity) of the reef community is exhibited by the fact that in several groups the nonphotosynthetic species, which are independent of light availability and hence should be able to grow anywhere, are rarely found in the upper parts of the reef. They increase in abundance and diversity only in the deep reef, although deep-water and nonsymbiotic species are often found in caves and other low light situations at shallow depths (30, 60, 123). Gorgonians with symbiotic algae dominated the gorgonian fauna to a depth of 55 m, where nonsymbiotic species became predominant (65). The same pattern occurs on a Florida reef (41), although the nonsymbiotic forms became abundant at a shallower depth, perhaps because of reduced water clarity. Sponges, most of which are nonsymbiotic, also increase in abundance and diversity with depth, as do nonphotosynthetic corals (46).

The pattern of diversity along the depth gradient of light availability also occurs along light gradients at much smaller scales. On the Great Barrier Reef, several species of *Acropora* have a table-shaped growth form, with a strong light gradient from the edge to the center of the shadow cast by the table. The number of coral species found in the shadow is low at the center and edge and highest in the zone of intermediate light levels (109) (Figure 4).

All of these patterns are consistent with Slobodkin's experiments (112) with hydra that showed that under high-light conditions a symbiotic species out-competed a nonsymbiotic species, but both coexisted at low-light levels. Thus it appears that fast-growing photosynthetic species may exclude nonphotosynthetic and slow-growing species from the upper parts of the reef, while conditions of slow growth in the deeper reef and turbid shallows allow the coexistence of many species.

THE INTERACTION OF COMPETITION AND DISTURBANCE

Coral reefs are influenced by a variety of physical and biological processes that may have opposing effects on species diversity. High growth rates of coral and algae in shallow water lead to intense competition for space and reduced species diversity, the result of dominance by competitively superior species. A variety of physical disturbances can increase diversity by reducing the population size of the dominant species, but even when physical conditions maintain high diversity on the reef crest, diversity increases with depth.



(DATA FROM SHEPPARD, 1981)

Figure 4 Relationship between number of coral species and position in shadow under table-like *Acropora* species on the Great Barrier Reef, Australia. The lower two curves are the average number of species per radial zone (all zones are of equal width, and therefore decreasing area toward the center) under tables of *Acropora cytherea* (▲) and *A. hyacinthus* (○). The two upper curves (●) are the total number of species found in each zone. The dotted curve is adjusted for area by dividing the total number of species by the total area sampled per zone. Based on data from Sheppard (109).

While tide, wave, and storm damage can have dramatic effects at the reef crest, the general pattern of increasing diversity to 20–30 m occurs regardless of the intensity of these disturbances. On a barrier reef near Barbados, Ott (89) also found similar levels of diversity on both the outer and the inner slopes. In a study of diversity on the Chagos atolls, Sheppard (108) found identical patterns of species richness along a depth gradient on both the seaward slope of the atoll and on the inner lagoon slope, where wave disturbance was greatly reduced.

This evidence suggests that the ubiquity of the depth gradient of diversity is

probably associated with the single physical gradient that has the same relative shape on all reefs—that is, the gradient of decreasing light availability with depth. Sheppard (108) noted that the highest diversity in his seaward transects occurred at sites (20 m) where the intensity of disturbance, either from surface waves or from silt-laden upwellings, was least. This observation is contrary to the basic prediction of the intermediate-disturbance hypothesis, which is that low diversity occurs at low disturbance frequencies. However, when the reduced growth rates at these greater depths are considered, the actual diversity patterns are consistent with predictions based on the interaction of growth rate with disturbance frequency.

Competitive interactions in the low-disturbance environment of the deep reef are clearly on the equilibrium end of the spectrum of nonequilibrium conditions. In fact, it would be difficult to distinguish a true equilibrium from a slowly changing nonequilibrium situation without detailed long-term study. Even in a system that would ultimately reach equilibrium, nonequilibrium coexistence can be prolonged by slow rates of change and high similarity between species (17). Extensive monospecific stands of *Montastrea* or *Agaricia* indicate that a low-diversity equilibrium can occur in the deep reef at depths where higher diversity also occurs. Very slow growth rates at these depths slow the rate of approach to equilibrium, which could ultimately be attained in the absence of disturbance.

Equilibrium can be approached much more rapidly in the upper parts of the reef, where a higher frequency of disturbance is necessary to prevent it from occurring. Not surprisingly, reef spatial patterns are much less constant near the surface than deeper in the reef (4). The low-diversity reef crests of *Porites porites* or *Acropora cervicornis* sometimes found on protected reefs may represent competitive equilibrium achieved in the absence of disturbance.

Reef diversity patterns resulting from the interaction of growth rates and disturbance frequencies are summarized in Figure 5. The concentric closed curves represent a contour map of expected diversity levels, with the highest values in the smallest closed curve in the lower-left corner. The pair of dashed lines that converge at the bottom of the figure encompass the range of physical conditions encountered at different depths on the forereef slope. Near the surface (0 m) the growth rates are high and the range of disturbance frequencies (and intensities) is great, reflecting variation in the degree to which the reef is exposed to or protected from storms and normal wave and tidal action. Growth rates are reduced with depth, and the frequency (and intensity) of wave action is reduced to low levels in the deep reef. The dashed ellipse represents the range of conditions at shallow turbid sites (generally in backreef areas or lagoons), where turbidity reduces light levels and, presumably, coral growth rates (which may also be reduced by the detrimental effects of sedimentation). Because these sites are close to the surface, the range of disturbance frequencies is greater than

at deeper sites on the forereef having the same light availability. Both shallow turbid sites and deep clearwater (forereef) sites may have the appropriate combinations of growth rates and disturbance frequencies to allow high levels of diversity.

The critical experiments needed to test the effect of variation of light and growth rate on community structure are technically feasible. Light levels can be manipulated using any neutral density filter, which may range from a window screen to an iron grating. Evaluating the interaction of light and wave disturbance would be possible at the low-disturbance end of the spectrum, where a platform (raised above water level to avoid fouling organisms) could shade a protected coral reef crest. Increasing light levels in the deep reef might be feasible but prohibitively expensive. Long-term manipulation of light (or anything else) becomes increasingly difficult as wave strength and frequency increase.

Alternative explanations for these patterns of diversity should be considered, but none of the most obvious seems appropriate: (a) The stability/diversity argument (113) is contradicted by the low diversity on reef crests with infrequent disturbances and by the nonmonotonic change with depth. This hy-

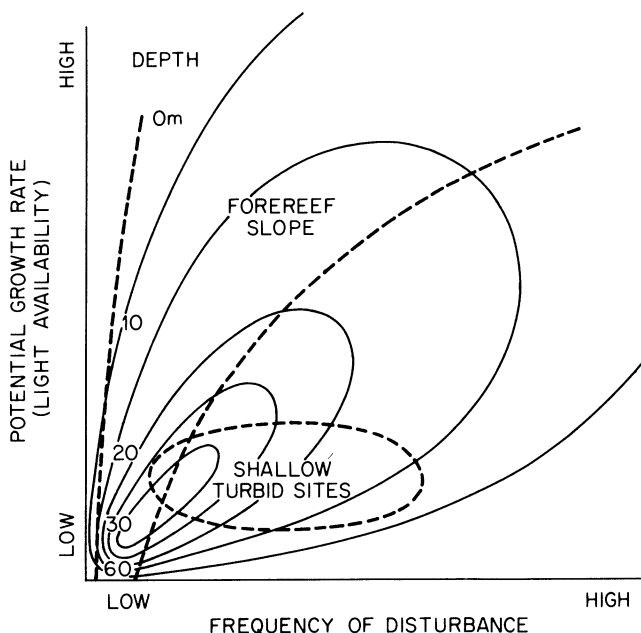


Figure 5 Putative relationship of coral reef physical conditions to predicted levels of species diversity resulting from the nonequilibrium interaction of growth rate and frequency of disturbance (based on Figure 7, 56). See text for details.

pothesis may be more appropriate on an evolutionary time scale than on the ecological one considered here. (b) It seems unlikely that diversity is controlled by limitations in the size of the species pool adapted to various depths, since most species are capable of growing over a wide depth range (Figure 2), including the shallow sites where they are rarely found. (c) Equilibrium coexistence based on finer resource partitioning in the diverse sites seems improbable given the disturbed and dynamic nature of coral reefs (18, 70, 130, 131).

Patterns of species diversity associated with variations in growth conditions and productivity have been described in a wide range of communities. High species diversity is associated with low (but not deficient) soil nutrient levels in terrestrial plant communities, including pastures and tropical forests (50, 57, 83). Diversity levels in understory plant communities show the same pattern in relation to light that is found on coral reefs (M. A. Huston, unpublished data). The ubiquity of these patterns suggests that similar processes may be controlling species diversity in a wide range of natural communities.

CONCLUSION

The sessile organisms of the coral reef form an archetypical nonequilibrium community whose structure is determined by interacting gradients of the rate of competitive displacement and by a range of disturbance types. The effect of these gradients is reflected in the remarkably consistent patterns of coral species zonation and species diversity found on well-developed reefs around the world. The coral diversity gradient, which increases with depth to a maximum around 20 m and then decreases with depth, appears to be associated with the gradient of light energy. Only the light gradient is consistent in direction and intensity on all reefs, and contrasts with a variety of biotic and abiotic disturbance gradients that are highly variable in intensity and also tend to decrease with depth. The effect of disturbance on reef community structure is interpretable only in the context of the rate of competitive displacement, which is equivalent to the rate of regrowth following disturbance. Growth rates of the photosynthetic coral and algae that dominate the reef are high near the surface, and a high rate of disturbances that reduce population size is necessary to prevent a few species from dominating. Diversity at the crest is low where disturbances are so frequent or intense that most species cannot survive, and low because of competitive displacement where disturbances are infrequent. Highest diversity is found at some intermediate frequency and intensity of disturbance. Even where disturbances are infrequent at the crest, species diversity increases with depth. This cannot be explained by the disturbance gradient, which inevitably decreases with depth, but is consistent with reduced rates of competitive displacement resulting from decreasing light availability and growth rates with depth. Below about 20–30 m, diversity begins to decrease slowly as decreasing light levels fall below the physiological limits of photosynthetic species.

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